Reference: *Biol. Bull.*, 149: 408–418. (October, 1975)

CAUSES OF DAILY RHYTHMS IN PHOTOSYNTHETIC RATES OF PHYTOPLANKTON. II. PHOSPHATE CONTROL OF EXPRESSION IN TUNDRA PONDS

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This paper continues to explore the cause and significance of daily photosynthetic rhythms in the phytoplankton. In earlier communications a model basis for the existence of an endogenous component in photosynthetic rhythms was described (Stross, Chisholm and Downing, 1973). The phytoplankton from the same lake (Lake George, New York) as elsewhere (Malone, 1971) has been shown to contain sub-components that function maximally at different times of day (Stross and Pemrick, 1974). In previous analyses rhythms were identified that were based on Michaelis coefficients resulting from the addition of various concentrations of phosphate. A photosynthetic potential was identified which measures the maximum stimulation resulting from the addition of a single, presumably rate limiting, nutrient. Reported here is an examination of the response of Lake George phytoplankton to nutrient enrichment at various times throughout the year. Secondly, the use of phosphate enrichment to identify daily maxima in photosynthetic rates was investigated in the phytoplankton from arctic pools.

A general model of the cell cycle includes a growth rate cycle only loosely coupled to cell division (Mitchison, 1974). In synchronous cultures of algae, cells divide at a predictable phase of the light-dark cycle, as is generally known. Nutrient limitation may permit only some of the population to divide at a scheduled time each day. Although cell division in such circumstances is a multi-day cycle, metabolic activities, as measured by phosphate uptake and photosynthetic rates, may oscillate with a daily frequency (Chisholm, 1974).

Application of a general model to an entire assemblage such as the phytoplankton has not been discouraged. Success of the so-called short term bioassay of Ryther and Guillard (1959) is proof that some species of the phytoplankton may readjust photosynthetic rate in response to nutrient enrichment within a 3 or 4 hour time span. Moreover, the coincidence of a maximum and minimum of photosynthetic capacity suggests that the most active taxa in the phytoplankton are synchronized (Stross *et al.*, 1973). An immediate feedback of the functional processes in all populations of the algae to resource availability is often postulated (Doyle and Poore, 1974; Ganf, 1974). Indeed, the environmental stimulus or driver is believed to be the cause of the rhythmic behavior of a functional process such as rates of uptake. The question, however, is to what extent does the amplitude and phase of oscillations in cellular activities such as cell division, nutrient uptake, and photosynthetic capacity of phytoplankton reflect the driving effect of external stimuli and to what extent are they predetermined by the

inherent characteristics of the individual taxa in the phytoplankton? The individuality of many species in culture is summarized by Senger (1970) and Chisholm (1974).

In the arctic and near arctic where the day is all lighted and the sun may be continuously above the horizon, evidence for rhythms in the activities of algae have included some of the most precise observations on field rhythms (Müller-Haeckel, 1970a, b; 1971). Rhythms in rates of cell division and attachment to substrata have been recorded for many species of algae that live in streams. Attachment rates of diatoms are demonstrated to be under the control of an endogenous clock (Müller-Haeckel, 1971).

The arctic coastal plain in northern Alaska where the study was conducted is characterized by low relief and elaborate development of a frost-patterned earth (Brown, 1970). Ponds may develop in the centers or between the polygonal patterns that result from frost action. In either case the ponds contain typical ecological communities, and the species are similar to those in temperate latitudes with the exclusion of vertebrates. Included in the community is a diverse assemblage of algae which has been intensively described for the area near the Arctic Research Laboratory at Point Barrow, Alaska (Kalff, 1967a, b; Alexander and Coulon, 1973).

Methods

Photosynthetic capacity was estimated as the net apparent rate of carbon fixation with minor modification of the standard technique. Samples of 100 ml were incubated for three hours on a revolving drum incubator (PECCER) at approximately 1500 ft-c and at the surface temperature of Lake George. In the arctic studies, either a revolving drum or cabinet incubator was employed at a temperature of 12° C ± 0.5 in each case. A correction of 1.43 × was applied for excretion by Lake George phytoplankton after extensive measurements (Downing, T. A., S.U.N.Y., Albany, unpublished manuscript). The arctic estimates were uncorrected.

Water from Lake George, New York was collected from 2.0 m beneath the surface immediately before the first of each time sequence of measurements. After passing through a number 25 mesh net (aperture = 64 micrometers), the water was transported and stored in 20-liter Pyrex carboys. The carboys, suspended at the surface of the lake and shielded from the direct rays of the sun, were agitated before removal of samples. Water from adjacent arctic pools (Ponds B and C USIBP Site 7) was collected from the pond surface and handled in a similar manner. The location of storage was at the Naval Arctic Research Laboratory, away from the ponds. The manner of storage was part of the experimental design.

At incubation, samples were enriched with phosphate only or with a "complete" set of nutrients routinely used for the culture of auxotrophic algae but more dilute (Stross *et al.*, 1973). Phosphate was tested at one or more concentrations ranging from 0.1 to 2.0 micromolar.

Statistical analysis consisted of a multiway analysis of variance and comparison of means (Sokal and Rohlf, 1969).

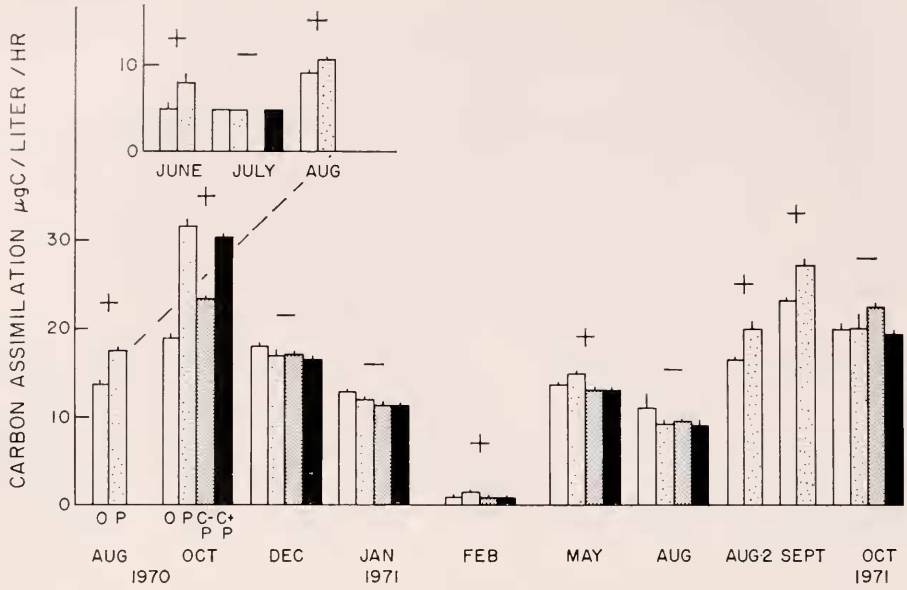

FIGURE 1. Rate of net carbon assimilation (PC) at 1500 ft-c and ambient lake temperature in response to nutrient addition. Shown are results from a sequence of tests beginning in June, 1970 and extending to October, 1971. Water was taken from Lake George, New York, station 1 and station 6 (upper left). Measurements were performed between the hours of 1000 and 1500. When phosphate stimulated ($P \leq .05$) photosynthesis, the sequence is marked with a "+". Symbols: O represents no additions; P, 0.25 or 0.5 μM PO_4 as sodium (primary) phosphate added; C-P, a complete nutrient solution added minus phosphate (see Stross *et al.* (1973) for details of the solution); C + P, complete nutrients including phosphate.

RESULTS

Continual bioassay of Lake George phytoplankton revealed that added phosphate stimulates photosynthesis as described earlier (Stross *et al.*, 1973). However, an apparent stimulation was observed on six of ten sampling dates only (Fig. 1). Hourly rates of carbon uptake ranged from 23.0 to less than 1.0 μg C/liter/hour. The addition of phosphate stimulated photosynthesis at each extreme of the range. There was, in other words, no clear association between the response to phosphate and the photosynthetic capacity of the phytoplankton.

A complete set of nutrients with or without phosphate was tested on seven dates at various times during the year. It was stimulatory on two occasions, once clearly the result of the included phosphate (Fig. 1; October, 1970) and once by some nutrient other than phosphate (October, 1971). Repetitive measurements were made on most of the sampling dates. The response was consistent however, and only the time of the expected daily maximum is shown in Figure 1.

The phytoplankton of the myriad small pools of the tundra near Barrow, Alaska is reasonably diverse in species but of extremely small numbers of cells (Kalff, 1967a, b; Alexander, Clasby and Coulon, 1972). Rates of photosynthesis at constant light and temperature ranged from 0.08 to 2.0 μg C/liter/hour in

the analyses reported here which began in 1971. Alexander and Coulon (1973) reported a considerable seasonal oscillation with a maximum after ice melt (mid-June) and again in the arctic autumn (August) of approximately 12 μg C/liter/hour. The minimum rates occurred in July, and their results are within the range of the rates reported here. Alexander and Coulon (1973) also report the dominant species of algae in the phytoplankton, which is dominated by species of the Cryptophyta and to a lesser extent by species of Chrysophyta and Chlorophyta.

Daily oscillations in the photosynthetic capacity are reputed to have small amplitudes in the arctic (Doty, 1959). The experiments were designed to detect an oscillation and to determine if the reputed small amplitude is the result of

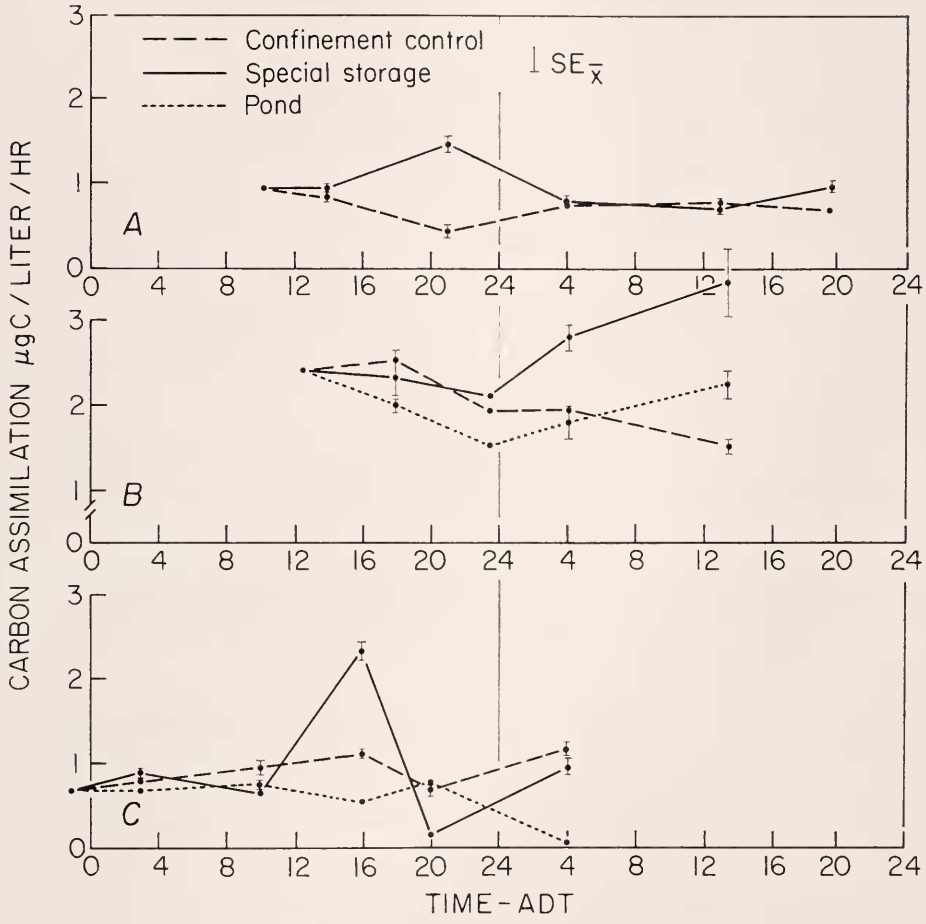

FIGURE 2. Daily time course of photosynthetic capacity (μgC/liter/hr) of arctic phytoplankton when samples removed from an arctic pond each time or from storage carboys exposed to daylight and varied temperatures (confinement control, spaced dashes) or from special storage (special, broken line). A, B and C are individual sequences begun on different days in July 1971 and started at different hours of the day. See text for details.

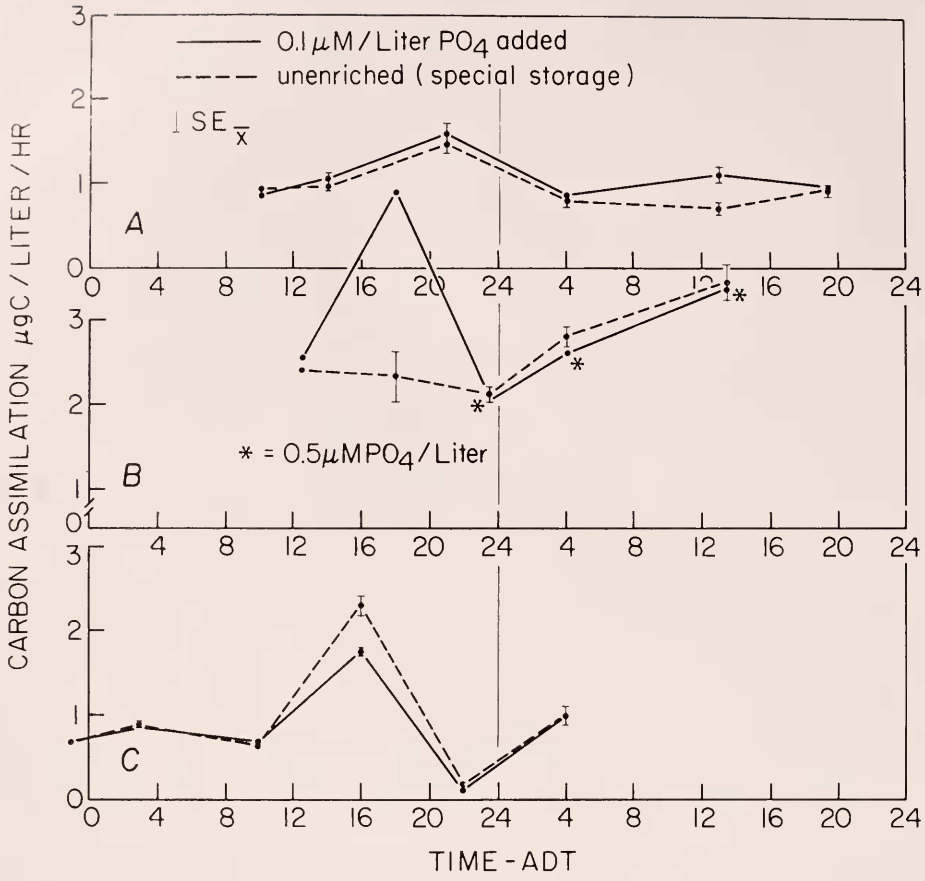

FIGURE 3. Photosynthetic capacity with and without phosphate enrichment added at the time of incubation. Unenriched controls (dashed line) are the special storage shown in Figure 2. Solid line shows a second part of the same sample when enriched with phosphate and incubated with the controls. Note that dramatic stimulation was restricted to only one of 17 measurements, that shown at 1800 in B.

extrinsic or intrinsic regulation. Two 20 liter carboys of water were removed from one of two tundra ponds at the beginning of each experiment. One carboy, the confinement control, was held outside of the laboratory usually shielded from the sun, when present. Samples from this carboy were paired with samples taken before each run directly from the pond. A second carboy was placed in a constant temperature (5° C) room at low light intensity (*ca.* 50 ft-c). The low temperature was similar to the morning minimum temperature of ponds at Barrow (71° N) where temperatures oscillate between 5° and 15° C on clear days.

Small fluctuations in the daily pattern of photosynthetic capacities were evident in samples taken directly from the pond (Fig. 2; dotted line) and suggest a small amplitude only. The confinement control also provided similarly phase indistinct, although statistically significant, fluctuations.

Large oscillations in photosynthetic rates were clearly evident in samples from the "stored" carboy. The peak in two of three runs was measured at 1600 and 2000. In a third run (Fig. 2B), storage in dim light-low temperature resulted in larger rates the following day, however. The late afternoon peak, although absent, was latent, as shown by the response to added phosphate.

Enrichment with phosphate (0.1 and 0.5 μM/liter) stimulated photosynthesis significantly on only one occasion in the three runs of July, 1971 (Fig. 3B). The single instance of nutrient-stimulated photosynthesis resulted in a distinct daily maximum in samples where a peak was expected.

It may be concluded that photosynthetic peaks in the arctic are suppressed. Special handling of the water samples allows expressions of a daily maximum, however, with amplitudes comparable to those observed at temperature latitudes. A common denominator in the successful treatment could be a charging of the algal cell with one or more nutrients. Although possibly coincidental, the special storage was insufficient in the run where placement of the carboy was delayed to mid-morning. Phosphate enrichment somehow substituted for the delayed storage. The time of the daily maximum, although not precisely determined, was in the vicinity of 1800. A "supper-hour" peak is later than is usually observed in temperate or tropical environments (Doty, 1959; Lorenzen, 1963; Malone, 1971).

A subsequent experiment was designed to test the inference that storage of the phytoplankton in a dim light-low temperature environment allows internal nutrients levels, specifically phosphate, to accumulate, thereby permitting faster rates of photosynthesis. Pairs of carboys were handled as above, one remaining exposed to the mostly indirect sun light, the second stored in constant conditions. One pair was started at 2200, a second at 0700 (ADT—Alaska Daylight Time). A fifth carboy was enriched with 0.1 μM/liter sodium (primary) phosphate and exposed to daylight with the confinement controls.

Photosynthetic capacity underwent a daily oscillation in the phytoplankton from all treatments (Fig. 4A). In the confinement controls, a peak of 0.11 μg C/liter/hour was measured at 1300 and nearly that at 1800. In the stored samples the daily maximum of 0.18 μg C/liter/hour was clearly at 1800 and apparently independent of the time the treatment began. In the "late storage" sample, the rate declined to a much lower level in the 2300 measurement (Fig. 4A).

A daily maximum was also evoked at the expected time in samples from the phosphate-enriched carboy. The rate, although less than in the two stored samples, showed the same general magnitude of increase from the previous measurement. The first measurement at 1300 was clearly suppressed below that measured in the confinement controls.

The pattern of response to phosphate enrichment although not completely consistent suggested that suppression of photosynthesis was characteristic the first day of confinement, while later measurements indicated stimulation (Fig. 4B).

A repeat experiment confirmed the major results. The daily maximum was again at or near 1800 ADT. Secondly, manipulation of the pond sample was essential to expression of the daily maximum. Thirdly, either storage in the special environment or preliminary enrichment with phosphate was capable of evoking the maximum. Fourthly, the addition of only 0.1 μM/liter phosphate was suppressive during the first day of confinement. In addition to confirming

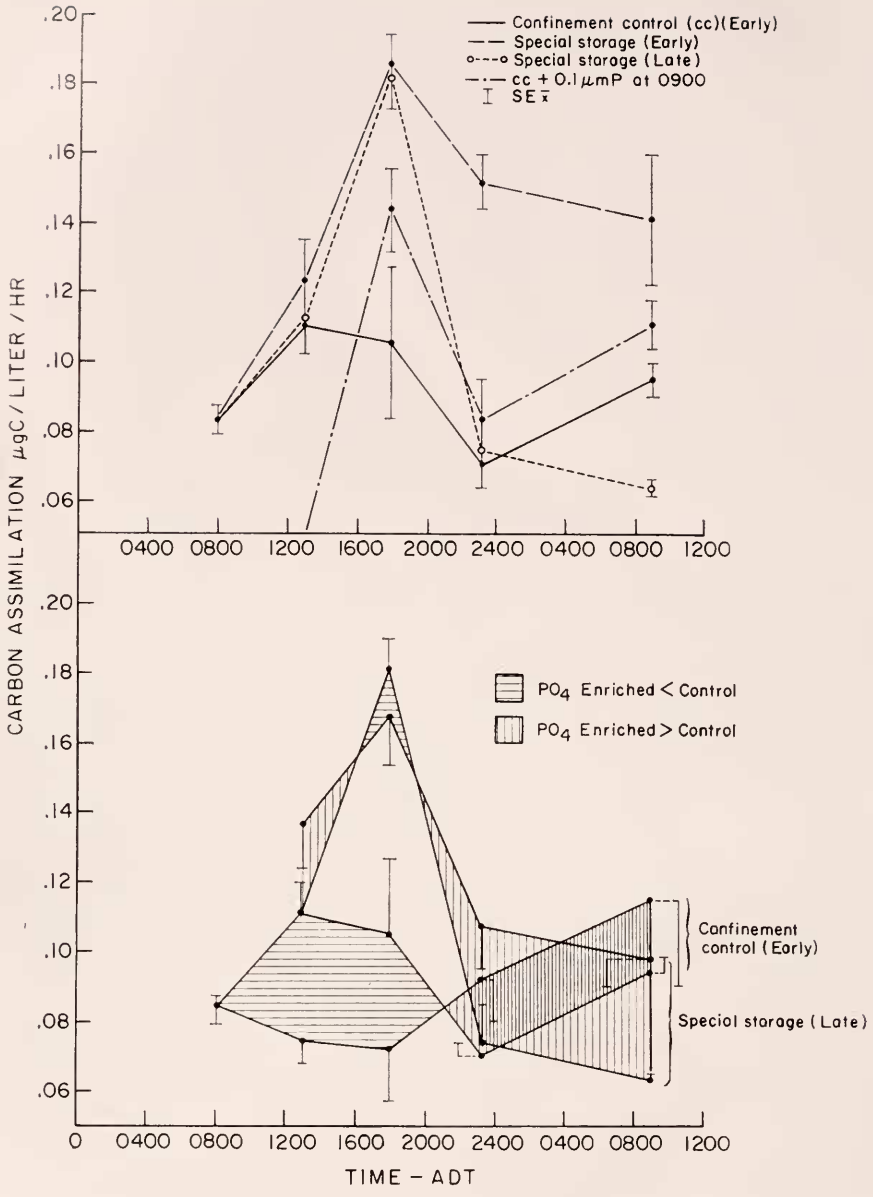

FIGURE 4. Daily time course of photosynthetic capacity in the first experiment of 1973. Shown (A) are the rates of photosynthesis in confinement control (solid line) as compared with rates following preincubation in dim light beginning at 2200 (dashed line) or 0700 ADT (dotted line). Compared also are the photosynthetic rates in samples taken from a carboy treated as a confinement control and enriched with 0.1 μM/liter sodium phosphate (dash — dot line). Compared in B are samples enriched with 0.1 μM/liter PO_4 with unenriched samples. Both confinement control and special storage treatments were chosen for comparison.

the first, the second experiment showed that although confinement and storage were made at 2100 on day zero the daily maximum took place at the expected time of 1800 on the day following.

Two general patterns of response were apparent in the three summers of observation. In 1971 and 1973 the daily maximum was late in the afternoon (supper hour). The immediate reaction to phosphate during the day was non-stimulatory and even suppressive. In 1972, photosynthesis was maximum in late morning or mid-day. Moreover, the addition of phosphate was generally stimulatory whenever samples were enriched. Both climate, which was warmer in 1972, or taxonomic peculiarities are possible explanations for the pattern differences in the time of the daily maximum and in the timing of the reaction to nutrient enrichment.

Discussion

Photosynthetic performance of the phytoplankton is similar in temperate lake and arctic pond. In each location photosynthetic capacity was observed to oscillate over the course of the day (Stross *et al.,* 1973 and above). In each location photosynthesis was stimulated within a three-hour interval following phosphate enrichment. Fertilization was effective on only some of the test dates, however. When not immediately effective with arctic phytoplankton, phosphate was still obviously stimulatory. Moreover, the restriction of a positive response to a particular time of day clearly implicates a biological rhythm. Interpretation of that rhythm is both critical and controversial.

Alternative viewpoints prevail as regards the cause of daily photosynthetic rhythms. One alternative views the phytoplankton as an externally driven system with or without a lag. Under its aegis, nutrient refractory rates of photosynthesis, as measured by the short-term bioassay (Ryther and Guillard, 1959), or decline in chlorophyll concentration as the sun rises in the sky (Yentsch and Ryther, 1957; *cf.* Ryther, Menzel and Vaccaro, 1961), can safely be viewed as direct responses to the nutrient and light environments. Morning "pulses" and afternoon "naps" imply direct reactions to a nightly increase in concentration of nutrient and photo-inhibition, respectively. Another alternative argues a certain freedom of responsiveness for the algae involved.

Extrapolation of the laboratory to the field permits a model combining endogenous rhythms with the kinetics of metabolic rates. Such a model allows metabolism to oscillate in a constant nutrient environment but with light-dark cycles. Nutrient uptake and growth rates are proportional both to concentrations in the external and internal environment and to the coefficients that relate uptake activity to substrate concentration (Dugdale, 1967; Caperon, 1968; Eppley, Rogers, McCarthy and Sournia, 1971; Fuhs, 1969; Rhee, 1973). However, the coefficients, for example, U_{max} and K_m are seen to oscillate with a daily periodicity in both saturated and nutrient limited cells of algae. Actual performance is then modified by the phase of oscillation, as demonstrated by Chisholm (1974). In other words, growth rate or rate of carbon assimilation is measuring both substrate concentration and phase of the daily cycle. O'Brien's (1972) models of growth are unrealistic because they do not specify physiological time dimensions.

An interpretation of the performance of arctic phytoplankton requires one more modification of the daily oscillation model. The "shape" of the daily oscillation

may need to be something different from the sinuosidal which has been used following the suggestion of Eppley *et al.*, (1971). Nutritionally charged phytoplankton, following incubation in sub-saturation intensities of light, developed a single pulse, often with rates three times larger than values taken previous to, or following, the peak. The single pulse was thus not more than a few hours in duration, at a predictable time of day, and was preceded by a long interval with a uniform rate. Within the latter interval is a period in which a nutrient may suppress rather than stimulate photosynthesis.

Cell division cycles in arctic algae may be phased to the earth's rotation (Müller-Haeckel, 1971). The presence of a daily maximum in photosynthetic rate is not surprising. Expression of the maximum is apparently uncertain and presumed to be nutrient limited since several manpulations were associated with the evening maximum in the experiments. Phosphate is suspected to be the limiting nutrient, since the addition of phosphate at an appropriate time was sufficient to stimulate an evening peak, albeit smaller than that which resulted from more elaborate manipulations.

It is the delayed, time-specific response to phosphate enrichment that argues for an endogenous phasing of the evening maximum. Why, for example, should samples exposed to light, although rarely direct sunlight, erupt at the same time as samples stored all day at only 50 ft-c? The delay in response to enrichment was also associated with the timing of the daily maximum. Peak rates in the vicinity of 1800 (ADT), the "supper hour," were observed as a part of a pattern that included a delay between nutrient enrichment and photosynthetic response on one hand, and a likely suppression in photosynthesis immediately following enrichment on the other.

A distinct pattern prevailed in 1972 and was different from that observed in the summers of 1971 and 1973. The daily maximum was near noon and the addition of phosphate usually stimulated photosynthesis within the three-hour incubation period. This latter condition of immediate response to phosphate may be the more typical of cultures in cyclostats (Chisholm, 1974), either because of the environment or the genotype selected.

An alternative explanation seems necessary to account for the typical pattern in arctic phytoplankton. The model described above may need to include a time coupling between the photosynthetic rhythm and a nutrient-controlled internal regulator of carbon assimilation. Such a model could simulate "a nutrient limited but rarely a phosphorus deficient, cell" (Peterson, Barlow and Savage, 1974).

A consequence of the time lag between enrichment and response is the need to reevaluate the so called short-term bioassay of Ryther and Guillard (1959). Only a positive response is open to interpretation. The question is how to modify a procedure that may require both a specific questioning and an answering time each day.

The implications of a time lag between phosphate enrichment and growth reaction are considerable, particularly if an endogenous rhythm controls the phase and amplitude of the growth maximum. Stability of the phytoplankton community becomes a property of the taxa that dominate the assemblage and only incidentally relates to qualities of the external environment such as the phase and amplitude of rhythms in nutrient concentration (*cf.* Ganf, 1974). The presence of a time lag

may allow the assemblage to appear to exist in a nutrient limited, but nutrient sufficient, condition as noted by Peterson *et al.* (1974). The obvious next step is to identify and culture taxa with time-specific demands and responses to external nutrient concentrations.

Appreciation is expressed to S. W. Chisholm and P. Starkweather. Members of the IBP Aquatic Group at Barrow offered valuable suggestions to the manuscript. Logistic support was provided by the Naval Arctic Research Laboratory. Project supported by NSF through AEC: AG–199, 40–193–69 and NSF Grant GV 29347 to Research Foundation of the State University of New York as part of the IBP Tundra Biome.

Summary

Experiments were carried out to determine if photosynthetic rates of phytoplankton were nutrient-limited in a temperate lake and in an arctic pond. They were also designed to determine if daily or seasonal patterns existed.

Photosynthetic rates were measured under defined light intensities and temperatures, at various concentrations of sodium phosphate. Daily patterns were determined with 5 or 7 measurements made over a 24 to 30 hour interval.

Photosynthetic rates were stimulated by the addition of phosphate to samples of water from Lake George, New York. They were stimulated on only some of the sampling dates during one year of survey. When phosphate was not limiting, neither were other essential nutrients, with one exception. Later work, in the arctic, suggested that a negative result should not be interpreted as a non-limiting situation, however.

Arctic phytoplankton show strong daily oscillations in photosynthetic rates. The daily maximum occurred most frequently in the early evening, at 1800; that is, at the supper hour. Manipulation of the samples was necessary to evoke the response.

The addition of phosphate, or storage of the samples in low light intensity, if done early in the day, was an adequate treatment to evoke the daily maximum. The synchrony of the peak under a variety of treatments was argument for the involvement of an endogenous rhythm rather than a direct environmental reaction.

The lag in reaction to nutrient stimulation is viewed as part of a mechanism to promote stability of the phytoplankton community and an obstacle in the interpretation of negative results from short-term nutrient bioassays.

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